

A Model for Temporal Sub-speciation

By R. L. H. DENNIS

This note is in appreciation of Mr G. Thomson's recent article on the same subject (antea: 87). I felt it might be useful to construct a model for temporal sub-speciation on current genetic theory, and it seems, on the face of it, that this is both possible and feasible. I hope then, that this note will provide a basis for any research into the subject, as well as explaining certain aspects of the whole phenomenon.

The main features of Mr Thomson's article were—firstly, the tendency towards a reduction in numbers in the univoltine brood in late August and early September, and the emergence of a second brood as a bivoltine inclination post that date; and secondly, the four major series of features (morphological) connected with the second brood which distinguish them from the usual series; these can be absorbed in the model.

The initial feature is the long flight period of *Maniola jurtina* (L.) (Satyridae), which is as he states occasionally from late June into the middle of October on the Isle of Wight. The model and the whole hypothesis demand a break in this sequence; an isolation barrier to divide a sympatric species into allochronic sections giving rise to sub-speciation. This can arise in the form of selective pressures operating in the middle of the flight period, which in the case of the Isle of Wight population would be slightly asymmetrical on the temporal scale (late August/early September). The whole process, however, can result initially as a genetic extension of a gaussian occurrence, assuming that the frequency of emergence in the flight period approaches this pattern. Certain specimens may occasion to emerge late via a random genetic endowment, and may, by mating continue the trend, but this would depend on a number of factors which need not concern us here. However, for the two broods to separate, as it were, a selection barrier preventing the continuum is essential. For speciation, an extension of the theory, a complete barrier to gene flow must develop, or be built up in the genome of either brood.

The model proposed here depends, or makes the initial assumption that the emergence time is governed by a series of loci and alleles, whether closely linked or not. In fact, though one would suspect more in reality, as many as two alleles for two loci may be utilized for our purposes here, since with increasing either of these, the simple model given becomes overcrowded cartographically.

With 2 alleles and 2 loci, nine genotypes are available. If this was to be extended to 3 loci, then 27 genotypes would be available and with 4, 81 genotypes, and this without altering the number of alleles, so it is evident, that with increasing the number of alleles and/or loci, a hoard of genetic variability is made available.

The genotype numbers are easily calculated from:—

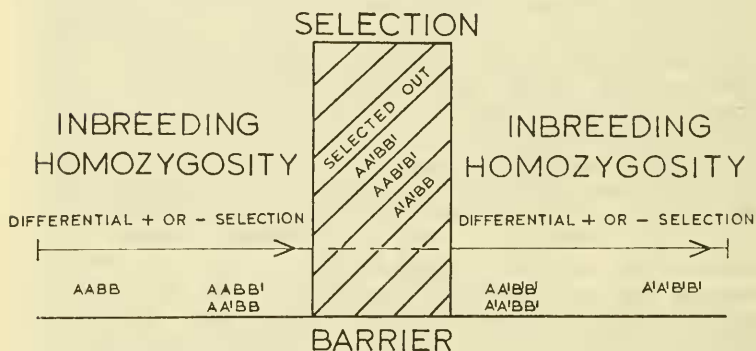
$$\text{Genotypes } N = \frac{n(n+1)}{2} \quad n = \text{alleles}$$

2

and with L loci, NL genotypes.

So, in our model, if we take 2 loci A and B with two alleles A/A¹ B/B¹ (without dominance effect, as with this small number of alleles and loci it would alter the results considerably) and allot to A and B early emergence, and to A¹ and B¹ late emergence, the system can be built up whereby there is selection against the intermediate genotypes, as indicated in the diagram, Fig. 1.

MODEL FOR TEMPORAL SUB SPECIATION



Selection, then, operates against A¹A¹B¹B, AA¹BB¹, AAB¹B¹, and A¹A¹BB in the model. The important function of the isolation (selection) barrier is that by separating two groups, it leads to inbreeding in the two allochronic populations, which in turn leads to homozygosity. Any intermediate values that these two broods produce will be eliminated, whilst if the late series produce 3 early facets, or in the early series 3 late facets, then these will add to the gene pool of the other, and avoid the barrier. In other words, gene flow does occur but operates to 'purify' the two broods. Of course in this simple 2 allelic/2 loci system, the end series contain so few a number of variables, that they cannot produce three facets that determine the other brood.

i.e., AA¹B¹B¹ × A¹A¹BB¹ can only give AA¹BB¹, AA¹B¹B¹, A¹A¹BB¹, and A¹A¹B¹B¹; the first of which ends up in the selection barrier and the final 3 in the late emergence category, from which they originated.

It will also be readily apparent that the two populations

now to a certain extent isolated may also be under different selective pressures themselves; quite different from the original selective barrier hypothesized. Two things might be happening in conjunction or separately. Either the features that are associated with the late emergence (such as smaller size, fulvous more extensive, UN considerably darker and more striate, and a smaller apical spot in the ♀♀) are part of the genetic endowment that distinguish the two groups temporally—I mean that the genes are pleiotropic in effect and that the genes for late emergence also affect other (morphological) differences—; or there is a second selective demand on the genome of the temporal populations that affects the frequency of certain genes also pleiotrophic for morphological characteristics. Finally both of these pressures may be operating in unison. It is interesting to reflect that both *Eumenis semele thyone* Thompson and *Plebejus argus caernensis* Thompson emerge earlier than their respective species colonies elsewhere in Great Britain, and are also significantly smaller. The important feature of the barrier is that the single brood no longer adjusts itself to the demands of the environment of the whole flight period, but is now separated into bivoltine units each deme separately adapting itself to the same spatial but temporally differential conditions.

A situation may also occur, unlike the negative pressures postulated on the bivoltine series above, but where the end ranges of the emergence sequence are favoured,—I mean in respect of the flight period without the selection barrier. However, even if this was so, it would still require some deleterious selection in the mid part of the range to allow the segregation of the two broods.

Of course this simple model leaves many questions unanswered. Among them, how many alleles and loci are operative, and what are the selection pressures? It is easy to see that with few loci, the effects of dominance, close linkage *et cetera* will have a profound effect on the model, and so with 2 loci, such a model would face severe difficulties. But with the geometric increase of genotypes, which can be calculated from the simple method I gave earlier, then with 4 loci/2 alleles, the amount of genetic variability would give the considerable range of divergence for the model to operate, even in the face of Mendelian offsetting or enhancing effects.

As for the selection pressures, these must be analyzed in the field. This population on the Isle of Wight differs by some factor(s) from other populations there. Perhaps the interesting point is not just the fresh late emerging specimens inclining to a second brood, but also the reduction in numbers that 'may or may not occur' at the end of August and early September. If this does indeed reflect on heavier selection in this period, through the multiple, as it were, we can follow the situation in the diagram. It will be interesting to see, as Mr Thomson points out, the numerical data associated with these

changes over a few years. It seems that with the close similarity in morphological changes associated with the late brood that a reasonably uniform mechanism is the cause of the phenomenon. It would be valuable to collect environmental data from these and surrounding colonies, from the macro scale of lithology, climatic data and notes on available food-plants *et cetera* in case these indicate effective forces; to detailed work on the differences through the flight period in the insects themselves.

It must be obvious by now, that there is a further possibility. The selection may not be in the mid part of the flight period at all, but may operate as selective selection on certain genotypes in the larval stage say; and the genotypes removed may be pleiotropic for the selective factor and mid flight emergence; i.e. the mid flight period emergence types (controlled by certain genotypes) may also be susceptible to selection pressures of a different nature much earlier in their existence, effecting the same genotypes. So it is wise to remember that in the diagram it is the *effect* of the selection barrier in the mid part of the flight period, though the selection itself may be operating at some other time of the year on a different stage of metamorphosis. On this note, the subject may for the moment be closed.

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A Review of the Butterflies of the Bristol Area

by A. D. R. Brown

(continued from p. 108)

Argynnis paphia Linn. (Silver Washed Fritillary)

Although the Silver Washed Fritillary is on the decline generally in the rest of the country, the signs are most encouraging in West Gloucestershire. Its potential in the Forest of Dean is tremendous, and we know of several good sightings from the areas around Monmouth. The situation is the same along the wooded areas of the Cotswold Hills, and we are just beginning to discover new haunts where it had previously been overlooked. In the Nature Reserve at Wetmoor, it is seen in most years but is not common.

Individual specimens have been seen from time to time at several places in North Somerset, but its future prospects do not look so good. It is probable that many of these isolated specimens have originated from the deciduous woodlands near Tickenham, but the M5 motorway development scheme has recently devastated this region. Once again, Goblin Combe is another well known locality for this species, but its numbers vary from one year to the next.